NOTES ON THE NATURAL HISTORY OF SPANGLEROGYRUS ALBIVENTRIS FOLKERTS, WITH A NEW DISTRIBUTION RECORD (COLEOPTERA: GYRINIDAE)

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The whirligig beetle *Spanglerogyrus albiventris* Folkerts (Coleoptera: Gyrinidae) was originally described from a series of 11 specimens taken from undercut banks of large streams at two localities in the Red Hills region of southwestern Alabama (Folkerts, 1979) and was reported to be uncommon at those sites. The species was placed in a separate subfamily because of its unique structure. Our interest in this small, aberrant gyrinid prompted a trip to the type-locality in April 1980 and resulted in the following report on its natural history. These observations may be helpful in future studies of gyrinid phylogeny and origin.

New Locality Record and Specimens

An intensive search of the type-locality near Peterman, Monroe County, yielded only 2 specimens of *Spanglerogyrus albiventris*, a female collected 11 April and a male on 17 April. Unusually heavy spring rains before and during our stay caused considerable flooding of streams in the area and we associated this with the low number of specimens taken. However, on 19 April at a nearby locality in Conecuh County (13 km E. Evergreen) we discovered a concentration of members of this species and took a series of 85 specimens (26 \Im , 59 \Im \Im) in about an hour of collecting.

This collection indicates that *S. albiventris* can be locally much more abundant than originally thought. The collection site represents the first record for the species in Conecuh County; it lies between and south of the two previously recorded sites and is within the presumed range figured by Folkerts (1979).

Cursory examinations of sex ratios in members of other gyrinid genera demonstrate that the high proportion of females to males is a common condition within the family.

Habitat

The large series of S. albiventris was collected midday at a shaded stream 8-12 m wide, with steep, mossy banks; surrounding soil is sandy and the

creek has a sand and gravel bottom. This is like the habitat described by Folkerts for the type-locality, but at this new site most of the beetles were concentrated near the mouths of two small tributaries (1–2 m wide) and up along the margins of one of them for more than 50 m; beyond that there were few suitable microhabitats, i.e. small undercuts and hollowed-out pockets in the bank. Highest concentrations were taken at the points of land at the confluence of the small creeks and main stream even though suitable microhabitats seemed equally distributed elsewhere along the margin of the large stream. Beetles were fewer in number and occurred in smaller isolated clusters as we sampled up the small creeks and fewer along the edge of the larger stream as we worked upstream and downstream from the mouths of the smaller ones. The absence of similar small tributaries at the type-locality might explain the low abundance at that site.

Our observations on the concentration of S. albiventris indicate that the presence of small tributaries to larger streams is probably an important factor in the maintenance of local populations of the species. We believe the larval habitat may be up the small streams rather than along the margins of the large ones. We did not find larvae, nor do we know when they are present. A few of the females examined contained 1-3 eggs, although most had none, suggesting that the eggs recently had been deposited.

We collected the beetles by wading in the stream and closely examining the margins where small shaded excavations of 5-10 cm in the bank or spaces among root tangles provided shelter from the current. *Spanglerogyrus* members usually were seen swimming rapidly on the water surface in these situations, singly or in clusters of up to 12 individuals depending on the size of the hollow or pocket. They were captured with a dipnet brought up to the surface from below. After being disturbed by the net, beetles not caught soon reappeared at the same spot.

The easy visual detection of specimens at this site, contrary to the observation by Folkerts, may have been due to the higher than normal water level; most of the larger shelflike undercut banks were submerged, thus forcing the beetles higher to more exposed habitats. On the other hand, relatively open microhabitats may be preferred. The species is apparently diurnal; activity in captive specimens decreases at night. The unpigmented venter, which may help to avoid visual detection from below by predators such as small fish, would be of particular advantage to a surface-dweller in open areas during the day. By comparison, species of *Gyretes*, which have a dark colored venter, are most often found under deep, shelflike banks where illumination is low.

Small body size may allow clusters of S. *albiventris* to utilize smaller spaces unsuitable for larger gyrinids and thereby allow them to avoid competition with the other species along the same stream bank. We collected *Gyretes* sp. at this locality in places similar and adjacent to those of S.

albiventris, but usually in larger, deeper pockets in the bank where S. albiventris rarely was found. Dineutus discolor Aubé also was taken nearby, in wide open areas, usually protected from strong current behind log-jams.

Behavior

We were able to observe the activity of *S. albiventris* both in the field and in captivity and to compare its behavior to that of members of three other gyrinid genera. In addition to the unusual jumping behavior described by Folkerts (1979), we noted some peculiarities not seen in other gyrinids. When associated with ecologic and structural features, these characters may be of help in understanding the position of *Spanglerogyrus* in the phylogeny and origin of the Gyrinidae.

Swimming.—The characteristic gyrating motion of gyrinids on the water surface is noticeably jerky and more rapid in S. albiventris, probably due to the comparatively small body size. The flat ventral surface of the body makes the beetle float like a bubble on the surface tension, having most of its body mass above water. Most larger gyrinids are convex ventrally and have relatively greater body mass below water level.

The single female taken 11 April was kept alive in a glass jar and closely observed for several days. The jar, 5 cm in diameter and 10 cm deep, contained water 5 cm deep and some emergent roots and pine needles from the stream. Swimming normally the beetle pursued a circular path 1–2 cm in diameter and made 2–4 revolutions per second. The beetle swam clockwise for an average of 4–12 revolutions, then reversed abruptly and swam counterclockwise for as many revolutions. This pattern was broken occasionally when the beetle would spin out in an exploratory manner, usually returning to the same spot to resume circling.

Diving.—Diving beneath the water surface, an evasive tactic often seen in other larger gyrinids, was observed also in S. albiventris. The small size, convex body form, and light build of these beetles appear to make them more bouyant; the captive specimens swam vigorously to remain submerged and soon bobbed back to the surface to resume gyrating. Members of S. albiventris made no attempt to cling to a root in order to stay submerged as is common in other gyrinids (Hatch, 1925a). The individuals observed seldom dived and appeared to do so only when highly agitated. In the field, specimens swam in wide zigzag paths and scattered when we approached, but dived only when directly disturbed. They dispersed temporarily along the stream margin but did not stray far from the pocket which they happened to be inhabiting; because of their comparative frailty it is possible that these beetles have a greater risk of being swept downstream by the current.

Feeding.—Spanglerogyrus albiventris is apparently a general surface scavenger and predator as are other members of the family; the gyrating

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habit aids the beetles in finding food particles. Bread crumbs dropped on the water were drawn inward by the circling of the beetle and were eaten as the beetle continued to swim. Group feeding on larger pieces of food was observed when we placed 15 beetles (from the series collected 19 April) in a jar and offered them some baetid mayflies. Several beetles surrounded and chewed at a floating mayfly while holding it with their front legs. One specimen of *S. albiventris* that had died in captivity was partially eaten by the others.

Some specimens preserved in alcohol immediately after collecting were dissected and gut contents were examined. Small fragments of dark colored insect (probably dipteran) exoskeleton were found.

Resting.—After feeding, the beetles swam to an emergent stem or root, or side of the glass jar, and climbed upward, then immediately turned around and rested with the head downward just above the water line. This habit and position probably facilitate rapid re-entry to the water. We were not able to observe *S. albiventris* at rest in the field (other than floating motionless on the water surface), but members of *Gyrinus*, *Gyretes* and *Dineutus* spp. were observed resting on emergent roots or in moss along the stream banks; the head-down position was rarely assumed, and does not seem to be characteristic of these genera.

Walking.—The long and relatively unmodified middle and hind tarsi of S. albiventris allow these beetles to be more agile out of water than members of other gyrinid groups. Captive specimens were observed walking steadily up stems and rootlets and across the glass surface of their container, and are capable of turning around on narrow stems such as pine needles. When walking the ventral surface is elevated, with only the tips of the tarsi contacting the substrate. All legs are used in walking, in the manner of cursorial insects.

On several occasions we saw a beetle reach the top of a stem and attempt to take flight, hit the side of the jar and fall to the water to resume swimming. The beetles spread their wings and took flight without jumping off the stem. The jumping behavior described by Folkerts (1979) is apparently used as a method of escape; we observed it only when beetles were caught in the net or placed on the ground.

Members of *Dineutus* often cling to floating leaves or emergent stems but rarely leave the water completely (Folkerts and Donovan, 1973) and we observed them doing so only under highly crowded captive conditions; the beetles that climbed available stems did so clumsily and often fell back into the water.

Members of stream-dwelling species of *Gyrinus* and *Gyretes* frequently climb up stems and twigs to rest and do so with proficiency (Folkerts and Donovan, 1973). The climbing is accomplished, however, by pushing with the short, flattened middle and hing legs and pulling with the long forelegs;

the body is not elevated above the substrate. We observed members of $Gyretes \ iricolor$ burrowing through moss on the banks of the streams, but neither this nor any of the above modes of terrestrial locomotion approach the actual walking of $S. \ albiventris$.

Unique Structural Features

Spanglerogyrus, which represents a monotypic subfamily, has many structural characters not present in members of other gyrinid taxa. Some of these may be considered highly derived, while others are plesiotypic, being present in other members of the Adephaga but not in other gyrinids. For comparison, Gyrinus, Dineutus, and Gyretes spp. plus representatives of some tropical genera were briefly examined; these genera represent each of the 3 tribes of the subfamily Gyrininae. Some important characters of Spanglerogyrus not previously recognized are noted.

An obvious difference in members of *Spanglerogyrus* is the lack of ventral excavations to receive the legs when folded. Distinct, trough-like excavations, particularly for the forelegs, are present in all members of the Gyrininae; members of Spanglerogyrinae have a nearly flat ventral surface. The shape of the dorsum in lateral view is also not as streamlined as in other gyrinids. These features of the general body form seem more typical of terrestrial beetles, and are probably associated with the walking behavior. The anterior coxal cavities, however, are like the type described by Bell (1966) for other Hydradephaga.

The mesosternum has an unusual shape and form: the posterior process between the mesocoxae comes to a narrow point, and the mesocoxae are nearly contiguous. In gyrinines this process is broadly bilobed (with a median emargination at the apex) and widely separates the mesocoxae. The anterior median carina in members of *Spanglerogyrus* is also absent in gyrinines. Since this mesosternal form is also distinct from that of other adephagans, it is considered here as an apotypic feature of *Spanglerogyrus*, but this is uncertain; further comparative studies in this area are needed.

The form of the metasternum is also radically different; it is relatively long and evenly transverse, whereas in gyrinines it is constricted and arcuate between the mesocoxae and the anteriorly expanded metacoxal plates. A distinct transverse sulcus on the metasternum, a character absent or weakly developed in other Hydradephaga (Bell, 1966), is present in *Spanglerogyrus* members. The metacoxal plates in *Spanglerogyrus* members are shorter and truncate anteriorly, and the femoral excavations are narrow and are oriented laterally rather than ventrally. These characters seem more carabid-like and are considered primitive.

The middle and hind legs in *Spanglerogyrus* members are modified for swimming differently than those of gyrinines, but seem to be equally effi-

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cient structures in both groups. In the gyrinines the tibiae and tarsi are shortened and flattened for swimming; in spanglerogyrines the tibiae have become greatly modified, while the tarsi, though equipped with long natatory hairs, have remained relatively unmodified. The long-fringed, oarlike, dorsal extensions of the tibiae in members of *Spanglerogyrus* are not known in any other aquatic beetles and must be considered as highly derived structures. The front tibiae, on the other hand, possess a primitive feature in having a distinct apical spur. Gyrinines possess at most a tuft of setae, but no protibial spurs. The front tarsi of male *Spanglerogyrus* are not strongly dilated and possess relatively few adhesive hairs, another feature considered less derived (Brinck, 1977).

In addition to the dorsal and ventral eyes being narrowly separated in spanglerogyrines, the dorsal eye is much larger than the ventral one; in gyrinines the reverse is true or the two eyes are roughly equal in size. In the hypothesized descent of the Gyrinidae, single compound eyes became divided as an adaptation for surface swimming, then the bridge between them widened as the dorsal eye moved upward. Extant *Spanglerogyrus* members possess the intermediate, less derived condition.

The apical visible abdominal sternum in spanglerogyrines is divided medially into two overlapping lobes, whereas gyrinines have an entire, broadly rounded or pointed abdominal apex. In both gyrinid subfamilies, this apical sclerite is the 8th sternum; the homologous sclerite in other known adephagans, usually also divided, is reduced and hidden beneath the 7th sternum, which is the apical visible sternum in these groups. An exposed and divided 8th sternum, a character unique to *S. albiventris*, might be considered a specialized (derived) feature. However, reduction, retraction and fusion of sclerites are generally considered to be derived states, while a more complex, unmodified condition implies an ancestral form. It seems more probable that the exposed, divided 8th sternum in *S. albiventris* is a plesiotypic character, retained since the origin of the gyrinid line.

The whiplike setae on the outer apical angle of the elytra are also unique structures. There are two equal adjacent setae on each elytron; they appear as single setae in dried specimens unless teased apart. In a surface-swimming beetle of small size they may be functional in keeping the water from covering the abdominal apex by breaking up the meniscus of surface tension around that region. Some gyrinines possess sharp spines along the apical margin of the elytra; these do not seem homologous to the setae in spanglerogyrines and probably have a protective function. We consider the elytral setae in *S. albiventris* to be a specialized apotypic feature because of their apparent functional nature, but it is possible that these setae are homologous to the tactile setae of the elytra in Carabidae. There are numerous tactile setae on the clypeus of *S. albiventris*; these are not typical of other known Hydradephaga. The presence of these setae and the other carabid-

like features in *Spanglerogyrus* members suggests a terrestrial origin of the Gyrinidae independent from other Hydradephaga, as was postulated by Bell (1966).

The presence of a setose median lobe in the male genitalia of *Spangler*ogyrus members is an unusual feature; median lobes in other gyrinids have no setae or accessory structures (Tranda, 1972). Although setose genitalia are generally considered a primitive feature, these short, retorse setae seem to be a specialized feature of male *Spanglerogyrus*. Also, the median lobe is not dorsoventrally flattened as in members of Gyrininae. The relatively reduced number of setae on the parameres also suggests an apotypic condition.

Conclusions

Many of the characters that give members of *Spanglerogyrus* their uniqueness seem to be related to small size, which is considered here as an apotypic character among the Gyrinidae. The extreme reduction in size is probably the result of specialization for a niche not occupied by other sympatric gyrinid species. We think the ability to walk and the associated physical features have been retained in *Spanglerogyrus* members because of the need for greater agility in a surface-swimming beetle with a smaller body size, which would be more vulnerable to sudden changes in its stream margin habitat. At the same time, spanglerogyrines have acquired natatory appendages (the oarlike meso-and metatibiae) equal in efficiency to the modified legs in other gyrinids.

The large dorsal eye which is not widely separated from the ventral eye, though considered a primitive condition, would also be advantageous for a small-sized surface swimmer. If *Spanglerogyrus* beetles live in small microhabitats close to the stream bank and are diurnal, as our observations suggest, a large, laterally oriented dorsal eye would be more useful than a smaller eye with a more dorsal orientation, as it would be easier for the beetles to orient themselves in a small semi-enclosed area while swimming and feeding.

We agree with Folkerts (1979) that the *Spanglerogyrus* taxon represents an early offshoot of the ancestral gyrinid line, but we do not think that the genus can truly be referred to as "primitive." Many of the apotypic characters of the genus (oarlike tibiae, whiplike elytral setae, form of the mesosternum, retorse setae of the median lobe, resting habit and jumping behavior) are not found in other known gyrinids and are not likely to have been features possessed by an early ancestral gyrinid. Although members of *Spanglerogyrus* do have plesiotypic structural and behavioral features that might be expected in an ancestral gyrinid, with its many other derived features it would not represent an example of the ancestral gyrinid form. We therefore suggest the unusual taxon *Spanglerogyrus* represents the plesion of Gyrinidae in terms of branching sequence, but has since acquired many autapotypic features.

The relatively primitive features of spanglerogyrines within Gyrinidae, however, may be useful in determining the origin of the Gyrinidae among the Adephaga. The walking behavior, setose clypeus, metasternal form, and structure of the hind coxae are more carabid-like than dytiscoid, supporting the view of Bell (1966) that the Gyrinidae arose directly from a terrestrial adephagan form, rather than an aquatic one. The male genitalia of gyrinids have characters that are generally considered to be plesiotypic, i.e. the dorsoventrally flattened, symmetrical, trilobed condition (Tranda, 1972). Asymmetry and reduction of the parameres are characteristic of caraboids, haliplids, and dytiscids, indicating that these groups are more closely related to each other than any of them are related to the Gyrinidae. This is contrary to the view of Hatch (1925b) and Crowson (1955), who have placed gyrinids near the Dytiscidae.

The complex of plesiotypic characters in *S. albiventris* implies a very early origin in adephagan evolution. We feel that the gyrinid line arose from a carabid-like terrestrial ancestor which gave rise to two main lines, the modern caraboids and the gyrinids. The dytiscoids and haliplids were perhaps a later offshoot of the caraboid line. In this proposed phylogeny, the Gyrinidae would be removed from the "Glabricornia" as defined by Bell (1966) and would become an earlier branch from primitive adephagan stock. An early common ancestor of modern Adephaga could have been similar to the one hypothesized for Bell's Glabricornia, but probably had male genitalia of the symmetrical, trilobed type, and an exposed and divided 8th abdominal sternum.

These ideas will be tested as more information is gathered from detailed studies of other aspects of life histories and internal structures. The discovery of the larva of *Spanglerogyrus* will be of great interest, in that it will provide another set of character states with which to analyze adephagan relationships.

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